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LOW SENSITIVITY TO PHOTOPERIOD MAY INCREASE POTATO YIELD IN SHORT DAY THROUGH THE MAINTENANCE OF SINK AND SOURCE BALANCE

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Abstract

Photoperiod is one of the environmental factors which affect the tuberization of potatoes. In order to determine the effects of photoperiod on tuberization of two potato cultivars, the effects of long (14 hours) and short (8 hours) days on the growth and production of mini-tubers in two potato cultivars (Agria and Savalan) were evaluated under controlled conditions. The results showed that plants grown under short-day conditions produced more mini-tubers, and these tubers were superior in terms of diameter compared to tubers grown in long days. Agria allocated more assimilates to shoots but lower assimilates to underground in long days which is economically more important. Savalan produced more tubers than Agria in short photoperiods, while, long photoperiod led to increase in shoot and decrease in root weight in this cultivar, still it was significantly higher than Agria. Chlorophyll content of both cultivars decreased under short photoperiod conditions. Irrespective to the cultivar, the number and length of stolon decreased under short photoperiod conditions, but the number of tubers per plant increased under such conditions. Savalan showed lower sensitivity to photoperiod than Agria. Therefore, in the photoperiod sensitive potato cultivars, production of mini-tubers in short days may be recommended, but in the long term, introduction of potato cultivars with lower sensitivity to photoperiod through plant breeding may increase potato yield in short days by maintaining sink and source balance.

Key words: Chlorophyll, Chlorophyll Fluorescence, Light Sensitivity, *Solanum Tuberosum* L., Tuber Yield.

Introduction

Potato (*Solanum tuberosum*) is a glandular crop that plays an important role in the nutrition of human beings (Eskandari *et al*., 2013). Global production of potato has been significantly increased and it is predicted that potato will become the most important agricultural crop in the food basket of the people in the future (Anon., 2005).

Tuberization in potato is influenced by both genomic and environmental factors (Sarkar, 2008; Kittipadukal *et al*., 2012). Allocation of assimilates is influenced by temperature, photoperiod, and genotype (Van Dam *et al*., 1996; Prat, 2010; Zahoor & Faheem, 2014; Aamir *et al*., 2016). Therefore, potato tuber production highly requires optimum temperature and day length, and is favoured by short photoperiods (Jackson *et al*., 2000; Fernie & Willmitzer, 2001; Hannapel *et al*., 2004; Prat, 2010). Tubers initiation in potato is stimulated more under short day than long day conditions (Koda & Kikuta, 2001; Sarkar, 2008; Jackson, 2009; Kittipadukal *et al*., 2012). Menzel (1985) stated that each potato cultivar has a specific critical day duration and in this critical day, irregular tuberization occurs but during longer days, tuberization is postponed or hindered (Menzel, 1985).

Although potato is a short day crop in terms of tuberization, there is a strong interaction between genotype and environment (Koda & Kikuta, 2001). On this basis, change in day length from short to long days brings changes to development of plant in terms of morphology and tuberization (Ewing & Warning, 1978).

Considering the fact that potato cultivation is common at different parts of the world with different day length, the less the sensitivity to day length, the higher yield of the plant is harvested. If the level of sensitivity to day length is high, the plant starts to form tubers very soon, before the shoot growth is enough to support the tubers operation, in short day regions.

On the other side, potato mini-tuber seeds are produced mainly in the greenhouse in which the day length can be controlled. In this study, we aim to analyse the effects of photoperiod on some physiological properties and minituber production of two commercial cultivars, Agria and Savalan under controlled conditions.

Materials and Methods

Experimental design: The experiment conducted in growth chamber Conviron 701 at Ferdowsi University of Mashhad, Iran, in 2015. The experimental design was factorial with completely randomized design layout with three replications. Treatments consisted of two cultivars (Agria and Savalan) and two photoperiods (long day with 14 h and short day with 8 h).

Plant material and growth conditions: Potato seedling were propagated using tissue culture technique, plantlets which had a length of about 8 to 10 cm and 4 to 6 nodes were selected and were transferred to pots. The seedlings of these cultivars were obtained from the Fanavarn Bazr Yekta Company.

Pots with 30 cm length and 10 cm diameter were filled with substrate of coco peat, perlite and sand in equal proportions and potato seedlings transplanted inside them. Then, pots were transferred to growth chamber with 16 h of day length and 8 h darkness, temperature was maintained at 23/20°C (day/night), relative humidity was 50-60% and fluorescent/incandescent lamps supplied 350 μmol m^{-2} s^{-1} at the top of the canopy. To feed the plants, the Hoagland's nutrient solution was used (Hoagland & Arnon, 1950). After two weeks of adaptation and establishment in the greenhouse, plants were transferred to two separate growth chambers, one with 14 h of day length and 10h darkness and the second with 8hours day length and 16hours darkness, with the same above mentioned environmental condition. Both groups of plants were grown for 85 days in these conditions.

Measurements: Relative leaf chlorophyll content was measured at 38 days after applying treatments by manual chlorophyll measurement (SPAD 502 Minolta, Japan). The chlorophyll fluorescence as an indicator of maximum efficiency of photosystem Ц was measured by using the OS1-FL flourimeter, 69 days after treatment.

After 85 days of treatments, all plants were harvested and then separated into leaves, stems, stolon and tubers. Leaf area (LA) was measured by leaf area meter (Li Core 3100, USA). Plant height, average leaf length, leaves and stem were oven dried for 48 h to measure dry weight. Dry weight of leaves and stems were added to calculate total shoot weight. Specific Leaf Area (cm2 g-1) was calculated using the following formulae:

$$\text{Specific leaf area } (cm^2.\ g^{-1}) = \frac{\text{Leaf area per plant } (cm^2)}{\text{Leaf weight per plant (g)}}$$

To minimize the damage to stolon and tubers, at harvest time, the pots were flooded for one hour to wash the roots. Then data for the number of tuber and stolon, the length of stolon and diameter of mini-tubers were measured.

Data analysis: Data were statistically analysed using the SAS software (SAS version 9.2). The least significant difference (LSD) test (p=0.05) was used to determine which treatment is statistically different from the others.

Results

Leaf area (LA): Analysis of variances indicated significant differences ($p \leq 0.01$) among treatments for leaf area (LA) (Table 1). LA of Savalan was higher in both photoperiods compared to Agria, and both cultivars produced higher LA at long days (LD) relative to short days (SD) (Table 2). Leaf area for Agria was highly influenced by photoperiod such that the leaf areas of Agria plants that are grown in LD-conditions were four times higher than leaf surface in SD-conditions, but in Savalan, there was no significant change in leaf area between two different photoperiods. It seems that in SD-conditions, most photosynthetic products are assigned to tubers, therefore, less assimilates are dedicated to aerial parts, hence, leaf surface decreases.

Table 1. Analysis of variance of different traits of two potato cultivars (Agria and Savalan) under two photoperiod conditions.

	Mean square			
	Cultivar	**Photoperiod**	**Cultivar × Photoperiod**	**c.v**
Leaf area	72385.3**	20122.83**	457070.36**	9.4
Specific leaf area	131461**	0.33 ns	16725**	14.71
Average leaf length	34.78**	0.285 ns	2.193**	2.58
Plant height	1573.23**	533.33**	255.637**	3.43
Leaf dry weight	0.0018 ns	0.448**	0.370**	12.9
Shoot dry weight	0.013 ns	11.23**	1.26**	7.76
Fv́/fm	0.0014**	0.0013*	0.00007 ns	1.65
Chlorophyll (Spad 32)	52.92**	27.60**	10.08*	2.84
Chlorophyll (Spad 34)	39.96**	17.04**	24.94**	2.7
Chlorophyll (Spad 36)	42.94**	42.18**	23.24**	1.32
Chlorophyll (Spad 38)	102.08**	82.16**	2.080**	1.19
Chlorophyll (Spad 40)	83.74**	85.86**	6.90**	1.96
Chlorophyll (Spad 42)	218.45**	81.12**	2.08*	1.22
Number of stolon	634.38**	3144.42**	1539.29**	3.95
Length of stolon	0.492 ns	12.27**	4.77**	15.21
Number of mini-tuber	10.212**	249.61**	15.43**	8.65
Mini-tuber diameter	0.473**	0.246**	0.252**	6.33

Table 2. Effects of photoperiod, potatoes cultivar (Agria (A) and Savalan (S)) and their interaction on leaf area (LA), specific leaf area (SLA), average leaf length and plant height in long (L) and short (S) days.

		LA (cm^2 $plant^{-1}$)	**SLA ($cm^2 g^{-1}$)**	**Average leaf length (cm)**	**Plant height (cm)**
Cultivar	A	179	187	10.5	105.3
	S	334	397	13.9	82.4
LSD (0.05)		32	57	0.4	4.3
Photoperiod	L	297	292	12.3	87.2
	S	216	292	12.0	100.5
LSD (0.05)		32	ns	ns	4.3
Cultivar× Photoperiod	AL	282	225	11.0	94.0
	AS	76	150	9.9	116.6
	SL	313	360	13.6	80.3
	SS	355	434	14.1	84.4
LSD (0.05)		54	81	0.5	6.0

Average leaf length: The effects of cultivars, interaction of cultivars and photoperiod on average leaf length were highly significant ($p \leq 0.01$) (Table 1). Savalan produced longer leaves than Agria. In Agria, longer leaves were produced in LD -conditions relative to SD -conditions, but in Savalan there was no significant difference between two photoperiods (Table 2). It shows that the size of leaves is another parameter that changes in response to photoperiod and cultivars Savalan has less susceptibility to photoperiod.

Specific leaf area (SLA): SLA in Savalan was two times higher than Agria cultivar (Table 2). However, Savalan produced more leaf area and thinner leaves than Agria. SLA in Agria was decreased about 33% in the short days compared to long day condition. These results showed that Agria strongly reduced its SLA in the SD condition, but Savalan showed different reaction and in short days, has thinner leaves compared to long-day conditions (Table 2).

Plant height: Height of Agria was significantly (27.8%) higher than Savalan (Table 2). The effect of day length on potato cultivars was also significant, ($p \leq 0.01$ such that in Agria, short day length produced taller plant (24%) than long day conditions. Yet; considering the height of the plants in Savalan, short day and long day conditions showed no significant differences (Table 2).

Relative chlorophyll content: The effect of cultivars, photoperiod and interaction of cultivars and photoperiod in all measurement dates on relative content of chlorophyll was significant (Table 1). Mean of SPAD number in Ageria was higher than Savalan. It was observed that plants grown in long day conditions showed more relative chlorophyll than those plants grown in short days. In both day length, by approaching the end of growth season, relative chlorophyll content decreased. In Agria in all dates, relative content of chlorophyll in long photoperiod was more than short photoperiod, but in Savalan cultivars, only 38 days after applying treatments (final stages of development), relative content of chlorophyll decreased (Table 3).

Chlorophyll fluorescence: The effect of photoperiod on F′v/Fm ($p \leq 0.05$) and the effect of cultivar on this trait was ($p \leq 0.01$) also significant (Table 1). Maximum effectiveness of photosystem II in Savalan was higher than Agria and in LD-length higher than SD (Table 4).

Table 4. Effects of photoperiod and cultivar on chlorophyll florescence leaf and shoot dry weight of two potato cultivars Agria (A) and Savalan (S) in long (L) and short (S) days.

		Fv́/fm	Leaf dry matter (gr)	Shoot dry weight (gr)
Cultivar	A	0.780	0.880	2.17
	S	0.800	0.850	2.10
LSD (0.05)		0.017	ns	ns
photoperiod	L	0.802	1.060	3.11
	S	0.781	0.670	1.17
LSD (0.05)		0.017	0.140	0.22
Cultivar× Photoperiod	AL	0.794	1.250	3.46
	AS	0.767	0.510	0.88
	SL	0.811	0.870	2.75
	SS	0.795	0.840	1.46
LSD (0.05)		ns	0.211	0.31

Table 3. Effects of photoperiod and cultivar on relative chlorophyll content of two potato cultivars Agria (A) and Savalan (S) in long (L) and short (S) days.

		Spad 32*	Spad 34	Spad 36	Spad 38	Spad 40	Spad42
Cultivar	A	50.2	48.4	47.8	47.26	47.0	48.0
	S	46.0	44.8	44.0	41.46	41.7	39.5
LSD (0.05)		1.8	1.6	0.8	0.70	1/1	0.7
Photoperiod	L	49.6	47.8	47.4	46.96	47.0	46.3
	S	46.5	45.4	44.0	41.76	41.7	41.1
LSD (0.05)		1.8	1.6	0.8	0.70	1.1	0.7
Cultivar × Photoperiod	AL	52.6	51.1	51.0	50.33	50.4	51.0
	AS	47.7	45.8	44.5	44.2	43.6	45.0
	SL	46.6	44.5	44.5	43.6	43.6	41.6
	SS	45.4	45.0	43.5	39.33	39.8	37.3
LSD (0.05)		2.5	2.3	1.1	0.9	1.6	1.0

* Numbers beside spade indicate days after transplanting

Leaf dry matter accumulation: The photoperiod effect on leaf dry weight of plants was significant ($p \leq 0.01$), and plants grown in LD condition had more leaf dry weight than those grown in SD conditions. The photoperiod effect on potato cultivars was also significant ($p \leq 0.01$), thus leaf dry weight of Agria in long day condition was 2.5 times higher than SD condition. However, Savalan didn't show any significant difference regarding leaf dry weight in SD and LD conditions (Table 4).

Shoot dry weight: Analysis of variance indicated significant differences among treatments for most of the traits including shoot dry weight ($p \leq 0.01$) (Table 1). Both cultivars grown in LD condition had more shoot dry weight than those grown in SD conditions. Shoot dry weight of Agria in long day condition have been increased about 4 times compared to SD condition, while shoot dry weight of Savalan cultivar in long days condition were about two times more than SD condition (Table 4).

Stolon number and length: Both photoperiod and cultivar significantly influenced the number and length of stolon (Table 1). More stolon was produced at LD conditions than SD conditions and in Agria relative to Savalan. Both cultivars in the LD condition produced more stolon compared to SD condition (Fig. 1).

Stolon in LD conditions was longer than SD conditions. Of course, Agria in the LD condition produced longer stolon and in the SD condition also produced shorter stolon compared to Savalan (Fig. 1).

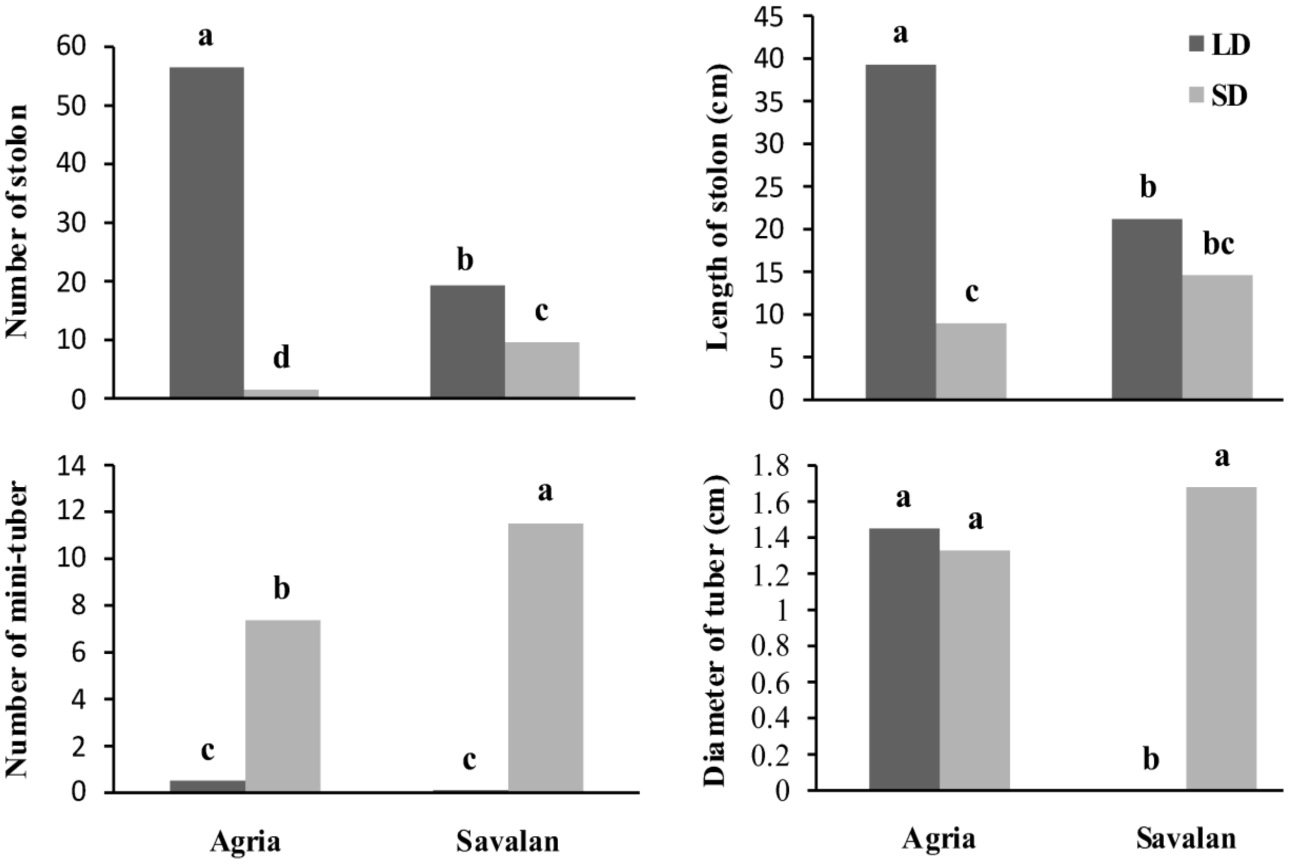

Fig. 1. The effect of photoperiod (long (L) and short (S) days) and cultivar on stolon number, stolon length and mini-tubers number and diameter of two potato cultivars.

Mini-tubers number and diameter: Since number of tubers per plant is important in producing mini-tubers, the effect of photoperiod, cultivar and their interaction was ($p \leq 0.01$) highly significant (Table 1). More mini-tubers were produced under SD-conditions relative to LD - conditions and in cultivar Savalan rather than Agria. Both cultivars in the SD condition produced more mini-tubers than LD condition (Fig. 1). Mini-tuber diameter was greater in cultivar Agria in comparison to Savalan and in the SD condition compared to LD (Fig. 1).

Discussion

According to the results, increasing plant height and tuber formation occurred under SD condition compared to LD. All these changes may be related to Gibberellin response in potato. Previous studies showed GAs effect on plant height, stolon growth and leaf properties. Also this hormone has a role in starch hydrolysis and assimilations movement (Prat, 2010; Bou-Torrent *et al*., 2011).Bou-Torrent *et al*. (2011) suggested that production of Gibberellin in long photoperiod hinders tuberization. According to Martínez-García et al. (2001), Gibberellin plays an important role in controlling tuberization process. Their observation showed that application of GA_3 hinders tuberization **(**Ewing & Struik, 1992; Jackson & Pratt, 1996; Fernie & Willmitzer, 2001), while using Gibberellin synthesis inhibitors initiate tuberization (Vreugdenhil *et al*., 2011). Bou-Tornet *et al*. (2011) also studied the effect of Gibberellin in controlling potato tuberization and stated that potato requires short days for tuberization and this process has reverse relationship with Gibberellins.

Most researchers also observed that in long day conditions, stolon produced in potato become longer (Prat, 2010; Vreugdenhil *et al*., 2011). But in short day, amount of GA20 to GA1 conversion increased in leaves. Therefore, amount of GA20 transport declines and then GA1 in stolon decreases and tuber formation occurs. Lorenz & Ewing (1992) stated that short day conditions lead to better tuberization in plants and in premature genotypes, it is accomplished with more power in comparison to Serotinous species. They observed that tuberization starts eight days after imposing to short day conditions.

In this study, by enhancing tuberization in SD condition, leaf weight, relative chlorophyll content, Fv́/fm and shoot weight decreased. These changes may cause by assimilate movement from shoot to tubers. Ewing & Struik (1992) also stated that leaves become thinner during tuberization, so the weight of leaves decreases. According to Ewing & Wareing (1978) there is an antagonist relationship between growth of branches and potato tuberization.

There are different photoperiodic responses between Savalan and Agria cultivars. Savalan had lower sensitivity to photoperiod than Agria. In Agria, changing from LD to SD condition leads to decrease in LA, SLA, SPAD, Fv́/fm', leaf and shoot dry weight, stolon numbers and increasing plant height and tuber number. But in Savalan, these traits are less influenced by photoperiodic changes. This may be the reason of less tuber number production in Agria than Savalan, since low formation of stolon probably has negative effect on tuber number. On the other hand, considering the growing part attributes, and the fact that Savalan cultivar does not decrease its photosynthetic surface during SD condition, more assimilates were allocated to stolon and more tubers were produced. Regarding these results, Savalan cultivar has less sensitivity to day length considering the less fluctuation of shoot and root performance in LD and SD conditions produced more tubers and it is more recommended for areas with specific climates. Seabrook & Co-workers (1993) searched the best sequence for short and long day cycle in order to produce best micro tuber in Cultivars Jemseq, Katahidin, Russet Burbank, and Superior. They observed that development of tuber is highly influenced by cultivars and photoperiod, although the number of micro tubers in Jemseq cultivars was not affected by photoperiod but Katahidin and Russet Burbank cultivars, in long day-long day treatment, produced less micro tubers in comparison to short day-short day and short day-long day regime.

In conclusion, photoperiod can affect potato tubirization, but there are different photoperiodic responses among cultivars. Although changing from LD to SD in sensitive cultivars reduces photosynthesis capacity through decreasing leaf area and chlorophyll content, and consequently may reduce tuber yield, on the other side, allocation pattern changes from shoots to the root which is ideal in potatoes. Therefore, in the available photoperiod sensitive potato cultivars, production of mini-tubers in short days may be recommended but in long term, introduction of low sensitive potato cultivars to photoperiod through plant breeding may increase potato yield in short days by maintaining sink and source balance.

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